

RESPONSE OF *SALIX LASIOLEPIS* TO AUGMENTED STREAM FLOWS IN THE UPPER OWENS RIVER

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ABSTRACT

The upper Owens River channel has been used for decades as an aqueduct to deliver flows from the Mono Basin to the Los Angeles Aqueduct. This out-of-basin diversion has tripled the volume of flow in the upper Owens River and altered channel and floodplain morphology (e.g., channels have become wider, deeper, and straighter). These changes have influenced density, distribution and growth response of the dominant riparian tree, *Salix lasiolepis* (white willow). Compared to an upstream control reach, juvenile *S. lasiolepis* had significantly lower density in the reach receiving the additional flows. Mature *S. lasiolepis* trees in the augmented-flow reach had significantly lower areal cover and had high relative abundance of dead trees. The trees tended to be located farther from the stream and to be more abundant on floodplains higher above the stream water level. These patterns may result from physiological intolerance of wetter soils, and from avulsive channel straightening and physical removal of seedlings and trees from near-stream recruitment areas during high flow flows.

Radial growth rates of mature *S. lasiolepis* did not differ between reaches, but annual growth patterns did differ. Growth of the willow in the control reach increased significantly with annual flow volume and was frequently limited by low flows. Growth of willow in the augmented reach decreased with annual flow volume and was limited by very high flows. Flows that produced greatest growth were at the high range of the natural flows and low range of the augmented flows. Very high flows may produce saturated conditions that are not conducive to growth or survival. If flows were restored to natural levels, we speculate that *S. lasiolepis* would ultimately increase in density. Density would remain low, however, until the river-floodplain system re-equilibrated and until other factors that limit willow abundance (i.e., cattle browsing) were minimized.

Stream flow diversion has contributed to regional decline of riparian vegetation in the western United States. Within California, for example, most riparian vegetation along the Owens River (the main drainage of the eastern Sierra Nevada) had been lost because of flow diversion into the Los Angeles Aqueduct (Brothers 1984). This regional loss has stimulated study on the effects of flow diversion and on instream flow needs of riparian vegetation (Risser and Harris 1989; Stromberg and Patten 1990). However, far less is known about the effects of flow augmentation, a less common form of flow manipulation. The upper Owens River provides an example of this type of flow manipulation. A 17 km segment of the upper Owens River has been used for the last 50 years as an aqueduct that receives

and delivers flows from nearby Mono Basin to downstream Crowley Lake and ultimately to the Los Angeles Aqueduct. Ongoing adjudication has called for examination of the impacts of this out-of-basin transfer on the diverted Mono Basin rivers as well as on the flow-augmented upper Owens River. This study had two objectives: (1) to document effects of flow augmentation on the dominant riparian tree (*Salix lasiolepis*) along the upper Owens River; and (2) to identify factors other than flow volume that are related to willow abundance within the study area.

STUDY AREA

The upper Owens River arises in the eastern Sierra Nevada foothills (Mono Co., California) and meanders through a broad valley along a shallow gradient for much of its length. The wide floodplains are vegetated mainly by hydrophilic herbaceous species, tree willows (primarily *Salix lasiolepis*, white willow), and shrub willows (primarily *S. exigua*, coyote willow), with incursions of Great Basin shrubs (*Artemisia* spp., *Chrysothamnus* spp.; nomenclature according to Munz and Keck [1973]). A few kilometers after it emerges from the foothills, the river is augmented by flows diverted from the Mono Basin (Rush, Lee Vining, Parker, and Walker creeks) through Mono Craters Tunnel (Fig. 1). Flow augmentation began in 1940 and increased in volume in the early 1970's. Below the augmentation point, the river continues to flow through broad valleys for about 17 km before being impounded in Crowley Lake and diverted into the Los Angeles Aqueduct.

The study was divided into two reaches with similar valley morphology (Fig. 1). The control reach extends for ca. 2 km upstream from Mono Craters Tunnel, and the augmented-flow reach extends for about 2 km downstream from the tunnel. The area in the first few hundred meters below the tunnel was excluded from study, because local springs and beaver ponds have produced vegetation that is not representative of the general area. Reaches farther upstream and downstream were also excluded because their floodplain morphology differed from that within the study area (e.g., floodplains were wider in downstream reaches, while stream gradient was steeper in upstream reaches).

METHODS

Response of the willow species to flow augmentation was documented by comparing the following parameters between *S. lasiolepis* stands in the control reach and augmented-flow reach: (1) abundance and distribution of juvenile and mature willows; (2) annual radial growth rates of mature willows; and (3) relationships between stream

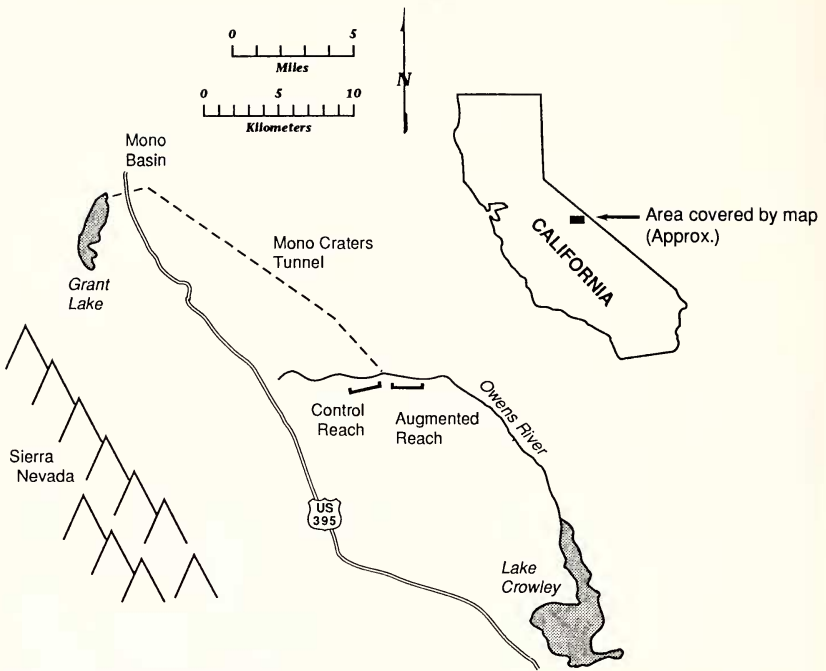


FIG. 1. Location of study reaches along the upper Owens River, Mono County, California.

flow volume and radial growth rates of mature willows. Data were also analyzed to determine to what extent factors other than flow augmentation were related to willow abundance. These factors included grazing intensity and factors potentially varying along a downstream distance gradient.

Density and distribution. Nine transects per reach were randomly selected and sampled in fall 1990 for density of willows. The transects spanned the width of the riparian floodplain and varied in width from 25 to 180 m. Willows were divided into two classes: juvenile plants (<1 m tall) and mature plants (>1 m tall). Density of the juveniles was sampled within 1-m wide belt transects (divided into 1×5 m plots) that spanned the width of the riparian zone. Plot number thus varied from 5 to 36, depending on floodplain width. Density of the juveniles also was sampled in an additional 50 streamside plots (1×2 m) randomly selected per transect, to obtain density values within main recruitment zones. Density and areal cover of live and dead mature willows were sampled in one large plot per transect that spanned the width of the floodplain and extended for 100 m in length. This unusually large plot size was chosen because of the low abundance of mature willows. Areal cover

was calculated based on two canopy diameter measurements per tree. For the density calculations, multiple-stemmed "plants" were considered as one individual.

Juvenile and mature willow abundances were compared between reaches and transects with analysis of variance to test the null hypotheses that abundances did not differ significantly between reaches. Within-reach relationships between juvenile and mature willow densities and five environmental variables (floodplain width, elevation of the near-stream floodplain relative to the stream, distance downstream within the reach, cow dung density) were determined with Pearson correlation analysis, using average values per transect ($n = 9$). Floodplain elevation was measured at five random locations per transect during a period of natural (i.e., unaugmented) flows (fall 1990). Density of cow dung "units," an index of recent grazing intensity, was sampled within the same floodplain plots sampled for juvenile willow density.

Radial growth. Increment cores were collected from ten mature *S. lasiolepis* trees per reach. The cored trees were randomly selected and had average canopy diameters of 7.1 ± 1.4 m (control group) and 7.2 ± 0.8 m (augmented-flow group). The cored trees had multiple stems, a common growth form for *S. lasiolepis*. Five cores were collected per tree, from large stems and from the main stem, if discernable. In the laboratory, the cores were mounted and sanded with a graded series of sandpaper (from 60 to 12 micrometers). The cores were cross-dated and measured for annual ring width with a Bannister-type incremental measuring machine. Many of the cored trees had "heart-rot" and only one of the chronologies pre-dated the onset of flow augmentation (1940). Fourteen of the 20 trees had chronology rings that extended through 1955, and these were used for subsequent analysis.

Average annual radial growth rate (over the period 1955–1989) was compared between reaches using analysis of variance to test the null hypothesis that growth rate did not differ significantly between reaches. Relationships between radial growth rate and stream flow (seasonal and annual flows) were analyzed by reach with univariate linear regression analysis. Streamflow data were obtained from Los Angeles Department of Water and Power. Flow data in the augmented-flow reach were for a gauge located immediately downstream from Mono Craters Tunnel. Data for the control reach were obtained by subtracting tunnel flows from augmented-reach flows.

RESULTS

Flow regimes. Natural flows in the upper Owens River averaged $52 \text{ hm}^3/\text{yr}$ (42,200 acre-feet/yr) and ranged from ca. 37 to $90 \text{ hm}^3/\text{yr}$ over the period 1941 to 1989 (Table 1, Fig. 2). During this period,

TABLE 1. COMPARISON OF FIVE ENVIRONMENTAL VARIABLES BETWEEN THE CONTROL AND AUGMENTED-FLOW REACHES OF THE UPPER OWENS RIVER.

	Control reach $\bar{x} \pm SD$	Augmented-flow reach $\bar{x} \pm SD$
Annual flow in water year (hm^3)	52 ± 12	$150 \pm 43^{**}$
Coefficient of variation in annual flow	24%	30%
Floodplain width (m)	101 ± 38	103 ± 54
Floodplain elevation above stream (cm)	34 ± 03	$41 \pm 8^*$
Cow dung density (no. m^{-2})	0.43 ± 0.15	0.36 ± 0.16

** P < 0.01.

* P < 0.05.

an average of $98 \text{ hm}^3/\text{yr}$ (range from ca. 17 to 180) were diverted from the Mono Basin through the Mono Tunnel. This tripled the flow volume in the augmented-flow reach, bringing the annual average to $150 \text{ hm}^3/\text{yr}$ (range from ca. 65 to 240). Annual fluctuation in flow has been higher in the augmented-flow reach, as indicated by coefficients of variation in annual flow: 30% for augmented-flow reach, 24% for control reach. Flow-augmentation has not altered seasonal flow patterns. In both reaches, more than half of the annual flow occurred during the May–October growing season (55% for control, 59% for augmented-flow reach), with peak flows in June.

Density and distribution of mature trees. Areal cover and density of mature *S. lasiolepis* were low in both the control and augmented-

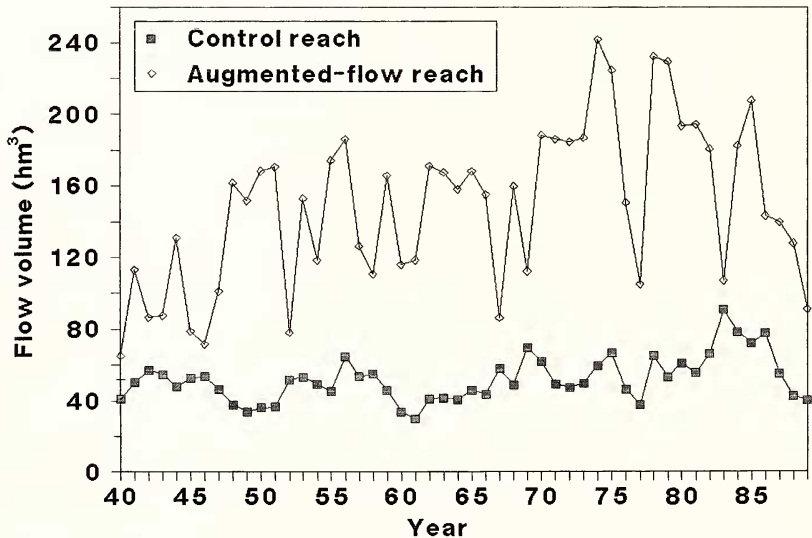


FIG. 2. Annual flow volume for the control and augmented-flow reaches of the upper Owens River.

TABLE 2. COMPARISON OF WILLOW VARIABLES BETWEEN CONTROL AND AUGMENTED-FLOW REACHES OF THE UPPER OWENS RIVER.

	Control reach $\bar{x} \pm SD$	Augmented reach $\bar{x} \pm SD$
<i>Mature Salix lasiolepis</i>		
Areal cover ($m^2 ha^{-1}$)	750 \pm 798	210 \pm 197*
Density (no. ha^{-1})	14 \pm 15	8 \pm 10
Live/dead density ratio	5.6 \pm 5.6	2.3 \pm 2.6
Distance to water's edge (m)	8.7 \pm 6.1	10.2 \pm 8.5
Radial growth rate ($mm yr^{-1}$)	2.43 \pm 0.75	2.82 \pm 0.63
<i>Juvenile Salix lasiolepis</i>		
Floodplain density (no. ha^{-1})	158 \pm 301	36 \pm 73
Streamedge density (no. ha^{-1})	2089 \pm 1789	233 \pm 283**
Juvenile/mature density ratio	209 \pm 221	67 \pm 128

** P < 0.05.

* P < 0.08.

flow reach. Cover values were significantly lower in the augmented-flow reach at $P < 0.08$, but densities of live trees did not differ significantly (Table 2). There were 2.3 live willows per dead willow in the augmented-flow reach compared to 5.6:1 for the control reach, but these values did not differ significantly. Willow trees on average occurred about 2m farther from the streamedge within the augmented-flow reach than in the control reach.

Density of mature *S. lasiolepis* decreased significantly with distance downstream within each reach (Table 3). These correlations were not significant, however, when the data were analyzed without three outliers with high willow density (Fig. 3). Density of the willow decreased with floodplain width within both reaches ($r = -0.75$ and -0.54). Within the augmented-flow reach, *S. lasiolepis* density was significantly correlated with floodplain height. Both reaches were heavily grazed (based on abundance of cow dung), and willow density

TABLE 3. CORRELATION COEFFICIENTS FOR *SALIX LASIOLEPIS* DENSITY AND FOUR ENVIRONMENTAL VARIABLES, FOR CONTROL AND AUGMENTED-FLOW REACHES OF THE UPPER OWENS RIVER.

	Distance downstream	Floodplain width	Floodplain elev.	Cow dung density
Control reach				
Mature density	-0.71*	-0.75*	0.18	-0.48
Juvenile density	-0.11	-0.33	0.06	-0.36
Augmented-flow reach				
Mature density	-0.63*	-0.54	0.63*	-0.19
Juvenile density	-0.01	0.18	-0.34	-0.23

* = P < 0.05.

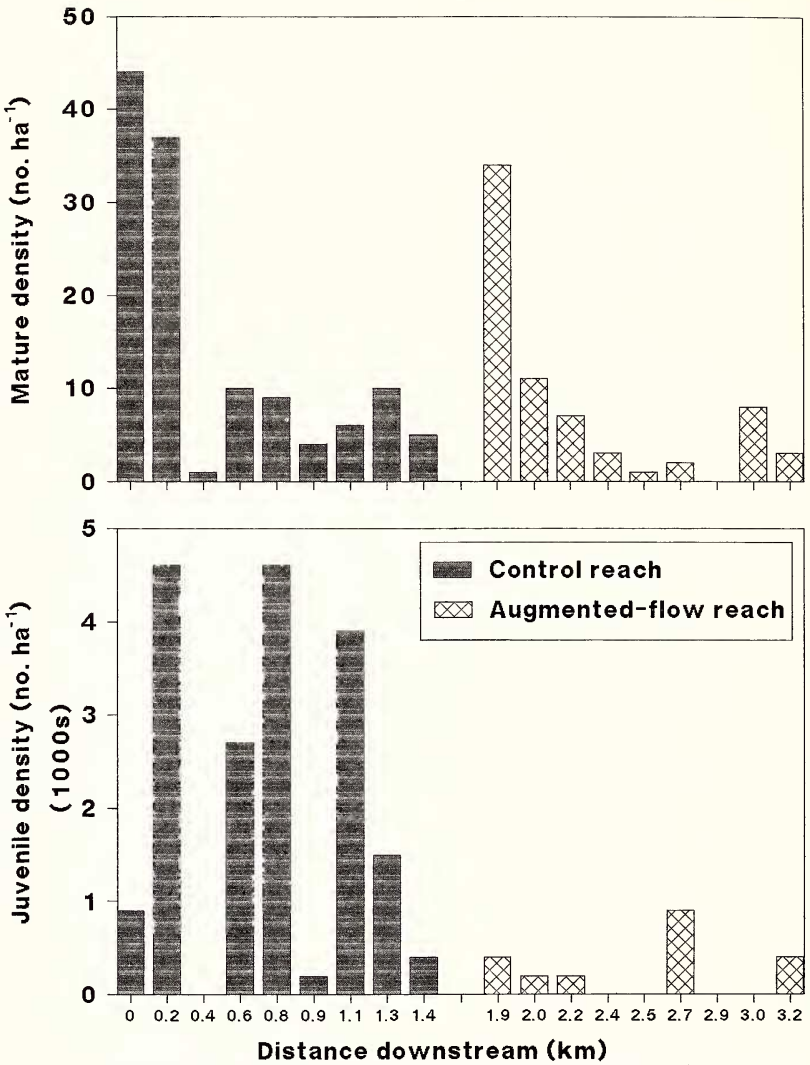


FIG. 3. Density of mature and juvenile *Salix lasiolepis* in relation to distance downstream from the upper end of the study area, for control and augmented-flow reaches of the upper Owens River.

tended to decrease with increasing density of cow dung in both reaches.

Density and distribution of juveniles. Densities of juvenile *S. lasiolepis* in both reaches were 10-fold higher along streamedges than in the floodplain as a whole (Table 2). Densities within this streamside recruitment zone were significantly lower in the augmented-

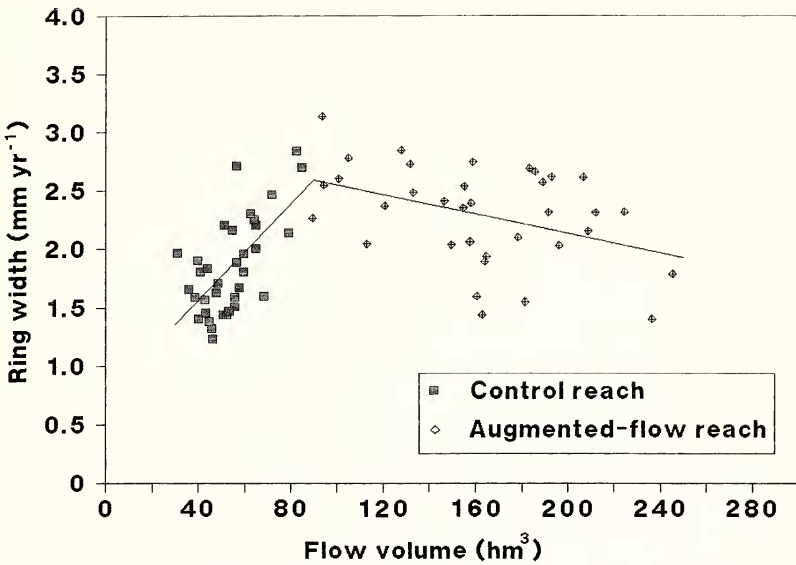


FIG. 4. Annual radial growth rate of *Salix lasiolepis* in relation to annual volume of flow in the water year (October–September), for control and augmented-flow reaches of the upper Owens River. Regression equations are: $y = 1.33 \pm 0.021x$, $r^2 = 0.49$, $df = 34$, $P < 0.01$ (control reach); $y = 3.48 - 0.004x$, $r^2 = 0.11$, $df = 34$, $P < 0.06$ (augmented-flow reach).

flow reach than in the control reach. The ratio of juvenile to mature individuals was >3-fold higher in the augmented-flow reach than in the control reach.

Observation indicated that most juvenile willows were browsed in both reaches. Many had relatively large diameter stems for their height, suggestive of repeated browsing. Juvenile willow density tended to decrease as cow dung density increased in both reaches, but correlations were not statistically significant (Table 3). Juvenile willows also tended to increase in density as floodplain height decreased within the augmented-flow reach, but again relationships were not significant. Density of juvenile willows did not vary with distance downstream in either reach (Fig. 3, Table 3).

Radial growth. Radial growth of *S. lasiolepis* in both reaches varied significantly as a function of stream flow volume, although in different fashion (Fig. 4). Growth rate of the willows in the control reach, where flow volumes were comparatively low, increased significantly with volume of flow during the October–September water year ($r^2 = 0.49$, $P < 0.01$, $df = 34$) and during the April–September growing season ($r^2 = 0.30$, $P < 0.01$, $df = 34$). In contrast, growth rate of trees in the augmented-flow reach declined as flow increased to high volumes, although relationships were less significant than in

the control reach ($r^2 = 0.11$, $P < 0.06$, for water year; $r^2 = 0.09$, $P < 0.08$, for April–September flow). Trees in both reaches had highest growth rates at “overlapping” flow volumes, i.e., those at the high range of the natural flows and low range of the augmented flows. Average annual radial growth rates did not statistically differ between reaches (Table 2).

DISCUSSION

Salix lasiolepis stands in the augmented-flow reach of the upper Owens River differed in several ways from that in the control reach. Juvenile willows had significantly lower densities in the augmented-flow reach. Mature trees had lower cover and tended to be present in lower proportion relative to dead trees. The trees in the augmented-flow reach had greatest abundance on floodplains highest above the stream water level, and grew somewhat farther from the stream than trees in the control reach. Growth of trees in the control reach increased with flow volume, and was often limited by low flows. The reverse was true for trees in the augmented-flow reach. Trees in both reaches attained highest growth rates at similar flow ranges (ca. 60–120 hm^3/yr).

Many of these differences in willow density and distribution may be attributable to flow augmentation. However, other factors also must be considered. Cattle effects, for example, complicate assessment of flow augmentation effects. Evidence in this study (i.e., the trend for negative correlations between cow dung and willow abundance) suggests that cattle grazing, browsing, and trampling has prevented willows in both reaches from attaining maximum potential densities. If true, this may have “dampened” changes wrought by altered flow regimes. Additionally, although the data is inconclusive, the possible trend for declining willow tree density with distance downstream raises the possibility that abiotic conditions are not uniform throughout the study area. For example, subtle changes in stream gradient or soil chemistry, or availability of suitable habitat for seedling establishment, may contribute to differences in willow trees within and between reaches. Thus, the weak trend for lower abundance of mature willows in the augmented-flow reach may not strictly be attributed to the altered flow regime. However, the low ratio of live to dead willow trees in the augmented-flow reach suggests that flow augmentation has played some role in increasing willow mortality. Mortality may have resulted from adverse physiological effects of excessive water or from physical removal of streamside trees in areas where flood flows have caused bank slumping and erosion. This latter phenomenon, combined with avulsive channel straightening, also may explain why trees were somewhat farther from the stream edge in the augmented-flow reach.

Juvenile willows, in contrast to mature willows, were significantly

less abundant in the augmented-flow reach and did not decrease in abundance with downstream distance within reaches. Furthermore, the ratio of juvenile to mature willows was several-fold more abundant in the control reach than in the augmented-flow reach. These data implicate flow augmentation as a primary factor that has reduced the abundance of juvenile *S. lasiolepis* below Mono Craters Tunnel. There are several possible mechanisms for this reduction. First, channel meanders have straightened and streambanks have undergone erosion and mass wasting (i.e., "slumping") as the river has adjusted to the new flow volume. This has physically removed sites where seedlings have established. Additionally, the high degree of flow fluctuation within the augmented reach may have increased seedling mortality rates (Strahan 1987). Another explanation may relate to availability of seedling habitat. Sand and gravel "point" bars are typical recruitment areas for *Salix* spp. (McBride and Strahan 1984), as was observed to be the case in this study (subjective observation). Such areas were not abundant in the augmented-flow reach, which has become an erosive rather than depositional environment, and which is characterized by steep banks, incised channels, and low rates of channel meandering.

Altered flow volumes are undoubtedly the primary cause for between-reach differences in annual radial growth patterns. Within the control reach, growth rate increased as flows increased, and flows never attained growth-suppressing levels. Such positive relations between flow volume and tree growth rate indicate that water availability can be a limiting factor in some riparian systems, as has been documented for riparian trees along streams in the eastern Sierra Nevada (Stromberg and Patten 1990, 1991) and elsewhere (Reily and Johnson 1982). This was not the case for the flow-augmented reach, where excess water availability apparently was a limiting factor. Reduced growth rates for *S. lasiolepis* at high flows may be a result of increased saturation within the riparian floodplain and reduced oxygenation to the root zone (Dionigi et al. 1985). Positive correlations between mature willow density and floodplain height in the augmented-flow reach support the idea that high flows have adversely affected growth and survival and suggest that growth and survivorship have been greater in higher, less saturated areas or areas subject to less erosive forces. The high degree of "scatter" between annual growth and flow in the augmented-flow reach may reflect topographical differences in annual saturation extent or genetic differences in saturation tolerance.

MANAGEMENT IMPLICATIONS

Although flow diversion is a more common scenario than is flow augmentation, there are many cases where an existing river channel is utilized as a natural aqueduct to deliver water between drainage

basins. In Arizona, for example, water from a tributary of the Little Colorado River is diverted into the East Verde River, as part of a system of water transfers designed to increase water supply at mining sites. Impacts of such water transfers on channel response (e.g., width and meander rate) have occasionally been addressed (Kellerhals et al. 1979; Bradley and Smith 1984), but impacts on riparian vegetation have received less study (Henszey et al. 1991). Effects of existing or proposed water transfers on riparian and aquatic ecosystems should be studied on a case-by-case basis, until generalizations are available relative to riparian community type, stream geomorphic type, and extent of change in stream flow regimes (Kondolf et al. 1987).

The data presented in this study indicate that flow augmentation has had adverse effects on the upper Owens River willow community. However, removal or reduction of the augmented flows would not instantaneously restore the upper Owens River willow community to its pre-perturbation state. We speculate that willow establishment will not become abundant until the river-floodplain system has re-equilibrated, which may take decades (Leopold 1964; Petts 1985). Reduction of high flows should decrease rates of willow mortality, but new recruitment depends on restoration of suitable floodplain morphology. Recovery of the willow population would be enhanced if cattle were at least temporarily removed from willow recruitment zones. In addition to allowing for new recruitment, removal of cattle would allow the existing juvenile willows to increase in size, thereby increasing their ability to stabilize banks and accelerate channel recovery (Armour et al. 1991). Further, this would ameliorate the adverse effects (e.g., increased water temperatures) on fish and other aquatic organisms that occur when riparian vegetation are not present to moderate stream temperatures (McGurk 1989).

Willow growth patterns should revert to "normal" once flows are restored to natural levels. Instead of being frequently limited by high flows, growth of the trees would be frequently limited by low flows as is presently the case in the control reach. Prediction of the extent of growth change is complicated by the changes in channel depth and floodplain height within the augmented-flow reach. These changes may have altered the relationship between stream flow volume and riparian water table depth, and between stream flow volume and growth rate. Nevertheless, existing information suggests that optimum growth of the willow trees would result from partial reduction in flow augmentation, to levels similar to those in the high range of natural flows.

ACKNOWLEDGMENTS

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